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THE UPPER PALEOZOIC FLORAS, THEIR SUCCESSION AND RANGE[1]

DAVID WHITE

VII

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STRATIGRAPHIC VALUE OF LAND PLANTS

Diastrophism and floral changes.—The terrestrial plant is inseparably dependent on the conditions, not only of the soil and the water, but also of the air from which it derives an important part of its substance. Any change, therefore, in the climatic, terrestrial, or water conditions of its environment directly affects the plant and causes morphologic changes to a greater or less degree, the greater plant variations corresponding usually to the greater environmental changes. The great floral revolutions of geologic history are connected with the great diastrophic movements.

Sensitiveness of land plants to complicated environment.—The land plant, being essentially without the power of locomotion except by accidental dispersion of its progeny, is most vitally susceptible to changes in composition, temperature, etc., of its environmental elements. Accordingly it constitutes a most sensitive indicator of changes in these elements. The more highly organized the type the greater, in general, is its value as evidence either for identity of environment or for altered conditions. It must be admitted, however, that in the interpretation of the environmental criteria afforded by fossil plants, relatively little serious study has been given to anything other than climate. The ecology of the fossil floras is a new and almost unexplored department of paleobotany, though splendid work along certain lines was begun by Grand'Eury. The results of differences in soils or in altitude have received little attention. In general the conditions of fossilization naturally presuppose the origin of the vegetal forms at an elevation not far from that of the water-level beneath which they have, in most cases, been preserved, though here and there certain types have been regarded as drifted from higher altitudes.

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[1] Published by permission of the director of the U. S. Geological Survey.

THE DEVONIAN FLORAS

Probable origin of land flora in Devonian.—From the paleobotanical standpoint no period within the existence of land floras is of such imminent interest and yet is so little known as the Devonian. This fact is no doubt due mainly to the relative rareness of indubitably botanical material, its usually fragmentary condition, or its partial obliteration through metamorphism. Yet the Devonian period probably covers the early development, if not the actual beginning, of terrestrial plant life on the earth. It witnessed the origin of ferns, scouring rushes, Lycopods, and Gymnosperms, including the earliest relatives of the conifers. It is supposed to have given birth to the Pteridosperms, a group of seed-bearing ferns (Cycadofices), standing in the gap between the ferns and the Cycads.

Features of early land plants.—The development in early Devonian time of flat land surfaces and low coasts whose bays were bordered by broad marshes intermittently covered by brackish or fresh waters was most favorable for the nearly simultaneous development of a terrestrial habit in some of the highly varied types which then populated the seas. On some accounts it seems permissible to suppose that the ancestors of the land plants were amphibious, perhaps growing where exposed only at the recession of the tide. It is, I believe, probable that these early plants were but sparsely foliate, their leaves being either spinoid or very small, slender, and delicately thin. The latter were probably dorsally rolled at first during the intervals of exposure to the air. The stomatiferous surfaces may have been very small for a time, and the stomata of periodic function only while the greater part of the carbonic-acid gas to serve as plant food was still drawn in the old way from the richly charged waters. The expansion of a proper leaf and the production of an aërial system of transpiration were presumably gradually evolved as the plant became weaned from its subaqueous habitat and accustomed to gain its food from an atmosphere which, it may be, was then better adapted to the nourishment of the emergent amphibian. However this may be it is fairly clear that the early representatives of the dominant Devonian types were of limited foliar expanse. Cuticular transmission of gases is still observed in the living ferns and Lycopods, the latter being far less susceptible to carbon-dioxide poisoning than are the higher plants.

It also appears that to support their weight in air a reinforced cuticle, later developed as a very thick and complicated cortex, was made to serve until a woody axis and, eventually, secondary wood should be fully produced by their descendants. From the characters of some of the fossils it seems probable that, unable to stand alone, they sprawled or clambered about on the ground or on other plants.

The mode of occurrence of their fossil remains usually in fresh or brackish water lagoonal or estuarine deposits, which are frequently ripple-marked, or even sun-cracked, may be regarded, though not without caution, as pointing out the conditions of their earliest habitats.

MIDDLE DEVONIAN

Characters.—The first Paleozoic land flora sufficiently known to make it eligible to the series of correlation discussions is that of the Middle Devonian.

This flora, whose apparent meagerness is perhaps due mostly to meagerness of information, is of strange and forbidding aspect. Its most characteristic types are Psilophyton, Arthrostigma, and Rhachiopteris of Dawson. It is also marked by the presence of Protolepidodendron, a primitive forerunner of the great lycopod group and, before reaching the Portage we find added Archaeopteris, together with the curious Pseudosporochnus, which may supply the missing fronds to the defoliated Caulopteris-like stems from Ohio and New York.

Place of origin.—Though eastern America has contributed most to our knowledge of this flora, it is probable that either the estuaries of northwestern Europe or the Arctic regions offered the conditions most favorable for its development. It extended both east and west in a high degree of unity. For example, the flora which occurs in the "Chapman" sandstone in Maine, and which is present in the gulf region of Canada, is largely the same as that of Scotland, at Burnot in Belgium, or in the Lenne shales of the Rhine Provinces. The flora from Barrande's *H-h*, stage at Hostim in Bohemia is nearly counterfeited in the upper Middle Devonian of New York. The route of migration between Europe and America was presumably by Arctic lands beyond the North Atlantic. Nothing that can be called a land flora is yet known from the Middle Devonian of the Southern Hemisphere.

UPPER DEVONIAN

Floral characters.—Evolution of forms and the advent of new types mark the Upper Devonian flora, which bears no evidence of any great climatic separation from the preceding. Pseudobornia, perhaps first of the Protocalamariales, Dimeripteris, Leptophleum, Barrandeina, and Barinophyton are characteristic. It is pre-eminently the stage of Archaeopteris. The Protolepidodendreae are developing along divergent lines to Cyclostigma and to the Carboniferous Lepidodendron, while Archaeosigillaria makes its rare appearance.

Place of origin and migration.—I am strongly inclined to believe that this flora received its greatest contribution from eastern America, or, perhaps, from the Arctic regions; in either event its migration was probably over boreal land; for it extends with remarkable identity from Pennsylvania to southern Europe and is partially present even in Australia. *Archaeopteris obtusa* and *A. sphenophyllifolia* of Pennsylvania and New York are *A. archetypus* and *A. fissilis* of Ellsmere Land, Spitzbergen, and the Don; while Barinophyton, a unique type from New York, Maine, and Canada, extends to the British Isles, Belgium, Queensland, and Victoria, where also is found *Leptophloeum rhombicum*, another American plant.

The Devonian woods present no annual rings to bear evidence of seasonal changes in temperature or intervals of prolonged drought.

THE CARBONIFEROUS FLORAS

MISSISSIPPIAN ("LOWER CARBONIFEROUS")

Characters.—The step from the Upper Devonian flora to that of the Mississippian (" Lower Carboniferous ") is marked by a floral contrast which, in some regions, is unexpectedly sharp though the warping of the Devonian floor to form the new Carboniferous synclines and the contraction of the seas naturally premise distinct climatic as well as other environmental changes. The new flora which lived in the restricted basins of the early Mississippian consists of Triphyllopteris, the broad, large-pinnuled Aneimites, the linear (*flaccida*) type of Sphenopteris, Cyclostigma, Eskdalia, and the acuminate Lepidodendra chiefly of the *corrugatum* group.

Lowest stage—Pocono.—The early Mississippian was a time of sea expansion; and in a number of distant areas, such as the northern part of the Appalachian trough, northern Alaska, the eastern Arctic, Scotland, and southern Siberia, the conditions at this moment were favorable for the formation of considerable coals.

Source.—Since the vegetation was presumably most luxuriant in these regions of coal formation, and since greatest evolution of forms attends most rapid and luxuriant expansion of a flora, we are perhaps safe in supposing that these are probably the regions of evolution of the flora as a whole.

Regional differences.—In this connection it may be noted that, either on account of land or marine barriers, or because the climatic conditions throughout the northern hemisphere may at the outset have been less uniform than in the preceding epoch, the different areas exhibit more or less distinct local floral differences. Thus in the Pecono of West Virginia and Eastern Pennsylvania where Triphyllopteris and the *corrugatum* type of Lepidodendron are almost without competition, the former achieved a remarkable differentiation far surpassing that known in any other area. In Nova Scotia, on the other, hand, the Horton series, which I regard as practically contemporaneous with the Pocono, contains the same Lepidodendra, accompanied, however, by Aneimites instead of Triphyllopteris. In both these regions the formations are in close relations with the Upper Devonian—in fact, probably in continuous sequence at one point or another. But the Pocono flora is apparently nearer to the Arctic

Alaskan where the same linear-lobed Sphenopteris forms are also present; the Nova Scotian affiliates more closely with the eastern. All the genera mingle in Arctic Europe and in Siberia, where Cyclostigma, probably of Arctic birth, has a good development. The Pocono flora may have connected by a more northern route with Europe, where Triphyllopteris sparingly mingles with the Horton Aneimites, which presumably migrated by the Northeast Arctic land bridge. It is possible, however, that some of the regional differences, especially differences in species, are due to lack of exact synchronism in the plant beds of these remote regions.

Middle Mississippian flora.—The basal Carboniferous floras are largely replaced in the middle Mississippian by a plant association which is more varied and of very different aspect. Where conditions were favorable for plant growth and preservation we find a flora essentially consisting of Rhacopteris (of Schimper, including Rhodea of authors), Cardiopteris, Asterocalamites (=Bornia), with *Lepidodendron volkmannianum*, and *L. veltheimianum*, accompanied by a gradually increasing group of Sphenopterids.

Source and distribution.—The middle Mississippian flora probably had its greatest development among the islands and estuaries of western Europe; at least it is best known in that region. From there it seems to have extended almost homogeneously to the eastward into Siberia and to the southeast, either through the Balkans, Persia, and the Himalayas (linking together its discovered occurrences), or possibly by a more southern route, to South Africa and Australia where the flora was largely identical with that in Siberia. The flora at Cacheuta, in Argentina, which though small is mainly composed of European species, presumably traversed the same route as that later followed by the Gangamopteris flora—that is the "Gondwana land." The middle Mississippian flora of the Appalachian trough is but little known, and for the most part is unpublished. Though less closely bound to that of Europe than are the corresponding Pennsylvanian floras its genera and a number of its species are present in the basins of Europe. I may add that the Megalopteris-bearing beds along the Mississippi River in Illinois, long ago credited to the Chester, are of upper Pottsville age.

Moderate uniformity of climate.—The members of this flora do not attain the gigantic proportions nor the specific differentiation of their Carboniferous successors; yet the relative homogeneity and the great radial distribution of this flora argue for the absence of distinct climatic zones in the recent sense while the apparent lack of annual rings, so far as the woods have been specially examined, is opposed to the idea of seasonal changes.

Upper Mississippian. Probable greater severity of climate.—Our knowledge of the flora of the uppermost part of the Mississippian is too insufficient, both as to its composition and its geographical distribution, to permit any very definite conclusions as to its province and climatic environment. Some at least of the plants exhibit a limited foliar expansion and semi-coriaceous character suggestive of conditions far less favorable for growth than in the Pennsylvanian ("Upper Carboniferous"), or even in the early Mississippian. They seem to forewarn us of the great floral change which was, perhaps, already in progress. From this highest stage may have come *Dadoxylon pennsylvanicum*, the only wood from the American Carboniferous which appears on authoritative testimony to show annual rings, but whose geologic age is unfortunately recorded merely as "Carboniferous." Also it is possible that the *Araucarites tchihatcheffianus*, from western Siberia, said to have been found in the Carboniferous limestone series, may belong to the same horizon. The occurrence of severer climatic conditions with seasonal changes within upper Mississippian time is provisionally admissible; but it is probable that a radical climatic change attended the post-Mississippian elevation, the maximum variation being presumably marked by the climax of the uplift. The paleobotanical revival which set in at the beginning of the Pennsylvanian is known to all. Even in regions of supposed continuous Mississippian-Pennsylvanian deposition the contrast between the older and the younger floras (which do not really come in contact) is very strongly marked.

PENNSYLVANIAN ("UPPER CARBONIFEROUS")

The Westphalian

Environmental changes.—Following the retirement of the sea from great areas at the close of the Mississippian ("Lower Carboniferous"), the new land surfaces were warped into new forms, with the production of additional as well as more complicated synclines. In these at first greatly restricted basins the sea began a great readvance, attended by the subsidence and deformation of the new basins under loading. These changes were most active during the Pottsville, the lowest of the American Pennsylvanian series. The new climatic and terrestrial conditions were most favorable to the extraordinary growth and differentiation of the plant life which spread across broad base-level plains and over the marshes and lagoons that flanked its long inland-reaching estuaries.

Appalachian deposition.—In the Appalachian trough the basin in earliest Pottsville time was confined to a very narrow estuary extending from the anthracite region of northeast Pennsylvania southward to Alabama where it became confluent with a small lobe of the sea extending northward toward southern Illinois and Indiana. Subsidence under loading was most rapid, with successive periods of sea advance to the north and west during all Pottsville time, at the close of which the water-level may have proximated its greatest Pennsylvanian extent; at least it exceeded the present limits of the coalfields.[1] The enormously expanded water-level of the Allegheny formation attended a westward migration of the axis of deposition, probably with the development of minor subordinate basins. Slight warping occurred during the period, especially to the southward, so that the connection with the Eastern Interior basin presumably migrated northward into the Kentucky region, foreshadowing the probable exclusion of the sea from the southern area of the present Appalachian coalfield during later Conemaugh and Monongahela time.

Rapid Evolution. Floral characters definite, with many short-lived genera in early Pennsylvanian.—The most rapid evolution of the Pennsylvanian flora occurred during Pottsville time, though the generation of new forms continued at a slower rate into the Allegheny, which, together with the Pottsville, approximately represents the Westphalian or Muscovian in North America.

The Westphalian is the period of Cheilanthites, Mariopteris, Diplothmema, Crossotheca, Eremopteris, Palmatopteris, Lonchopteris, Megalopteris, Lesleya, Neriopteris, Bothrodendron, Ulodendron, Lepidophloios, and Whittleseya, besides a number of genera representing filicoid types of fructification. One-half of these genera scarcely, if at all, survive the Pottsville. Three or four only outlive the Allegheny. The Westphalian witnessed the maximum development in Sphenopteris, Neuropteris, and Alethopteris, and of the great Lycopod group. It is pre-eminently the stage of the Cycadifilices.

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[1] *Bull. Geol. Soc. Amer.*, Vol. XV (1904), p. 267.

Remarkable distribution of identical species.—The intercontinental distribution of the Westphalian plants is probably less remarkably uniform than is generally stated. The examination of the floras shows minor differences between the floras of different basins, as, for example, freshwater or marine basins in the same country, though many of these differences disappear as additional material is collected. Also different areas in the same basin, and, similarly, different horizons in the same basin may show predominances of Lycopods, or ferns, etc., or the apparent absence of certain genera. But as between the larger provinces, and taking the flora as a whole, from continent to continent, the number of genera not common, for example, to Europe and America, is so small as to excite special interest. The proportion of identical species is so large as to necessitate an extraordinary lack of barriers to the freest migration. The flora of the basin of Heraclea in Asia Minor[1] lends itself to ready correlation, stage by stage, with three corresponding formations of the Pottsville in the Appalachian trough; also, of the 33 species reported by Zeiller in a collection from the Westphalian of the Djebel-Bechar region of Persia, 25 are present in the Pottsville of the Appalachian trough.

The uniformity of distribution of the Westphalian flora complicates the geographical question of its origin. Taking therefore as most reliable the evidence of first appearances, we may note that Cheilanthites (including portions of Pseudopecopteris and Sphenopteris), Mariopteris, Eremopteris, Neuropteris, Alethopteris, and perhaps Pecopteris, were more highly differentiated in America, though Sphenopteris experienced a perhaps greater development in Austria and Bohemia. In Europe the Lycopods appear to have had greater advancement. Also, Cingularia, unknown outside of the freshwater basins of Germany, and Lonchopteris, largely confined thereto, have not yet been found in North America; while the unique genus Neriopteris is still unknown in Europe. On the other hand, the rare genera, Lesleya, Megalopteris, and Whittleseya, apparently originated in America whence they spread northeastward. The same is true of the lower Pottsville Phyllotheca, which appeared a little later in Heraclea, and finally, in a new group of forms, became somewhat characteristic of the Gangamopteris flora of "Gondwana land." On the whole, therefore, it is probable that the Westphalian flora is the joint contribution of the lagoonal– i. e., coal-forming—regions of western Europe and eastern America. Free inter-communication was almost certainly by an Arctic land bridge, possibly by way of a Greenland-Scandinavian shore connection. The general regional distribution of the Pennsylvanian floras is shown in Fig. 1.

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[1] *Jour. Geol.*, Vol. IX (1901), p. 192.

The Stephanian

Conditions of deposition and probable equivalents.—The Stephanian or Ouralian (including the Gschellian) of Europe dates from the Hercynian uplift. Prior to this movement the sea had reached its maximum extension in the coalfields of the northern hemisphere. The Hercynian thrust caused its practical expulsion from the old synclines of western Europe and the creation, especially to the southward, of new basins, mostly of fresh or brackish water, to which were transferred the scenes of coal-formation. In America the line between the Westphalian and Stephanian is not yet accurately drawn, the fossil floras being not studied in sufficient detail. In view, however, of the paleobotanical evidence indicative of a point near the Allegheny-Conemaugh boundary, I, personally, am inclined to regard the formation of the Mahoning sandstone (conglomeratic), the changed sedimentation of the Conemaugh formation, the probable upwarp of the southern Appalachian region which later resulted in the exclusion of the sea from the northern area also, and the consequent climatic changes, as due to the same great orogenic influence. Accordingly I would provisionally place the greater part, if not all, of the Conemaugh together with the Monongahela in the Stephanian.

The final exclusion of the sea from the Appalachian trough appears to have occurred soon after the deposition of the Ames limestone, near the middle of the Conemaugh, since, according to reports, only fresh, or possibly brackish water mollusca occur in the higher terranes.[1]

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[1] I. C. White, *Report IIA*, Geol. Surv. W. Va., p. 622.

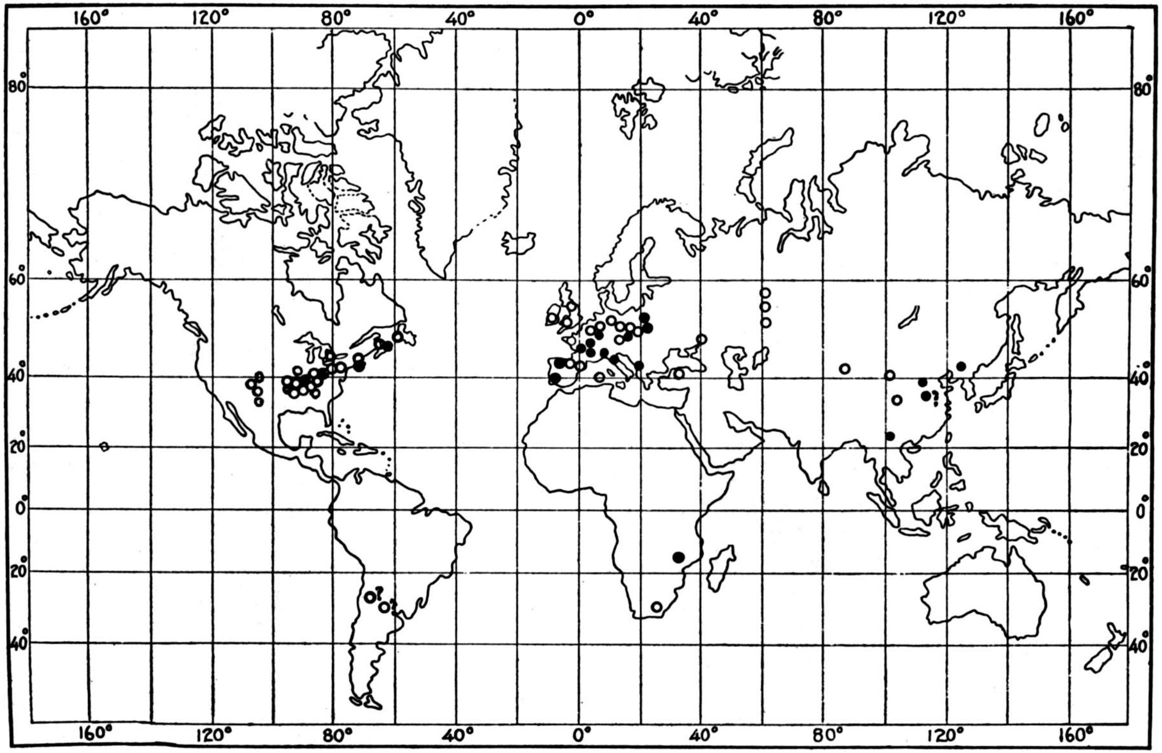

Fig. 1.—Regional distribution of Pennsylvanian ("Upper Carboniferous") floras. White rings = Westphalian plants; black rings = Stephanian plants.

It is probable that the Monongahela was never deposited in the southern Appalachian region, from portions of which the Conemaugh may also have been absent, the red oxidized sediments of the latter being in part derived, I believe, from the eroded unconsolidated older Pennsylvanian to the southeastward.

Floral characters.—The Stephanian is marked by the great development of Pecopteris, Callipteridium, and Odontopteris of the true type. It witnessed the nearly complete disappearance of Alethopteris, Sigillaria, and Lepidodendron. Neuropteris of the large-pinnuled forms enters its period of decadence. Before its close appear the first representatives of Callipteris, Walchia, Taeniopteris of the simple type, Pterophyllum, Zamites, and Plagiozamites, all characteristic of the Permian or later periods.

In eastern America, where the relations of land and water were but gradually altered and the sedimentation was continuous, the passage to the Stephanian flora has no line of sharp paleobotanical demarkation. The change appears to be gentle and the older forms drop out more slowly. In Europe, on the other hand, the contrast is a little sharper; the old types disappear more abruptly and many new ones take their places. A number of these new types have not yet been found in the Permian of this country. Among these are the four Permian coniferal and cycadalean genera above mentioned.

Source and distribution of the flora.—It is clear that the new elements of our Stephanian flora are chiefly, at least, of European origin, the plant life there having been directly influenced by the important physical changes to which it was immediately subjected. The various exotic types migrated to North America, probably, along or near the general route traversed by their Westphalian predecessors. Also, since the Stephanian flora of the American basins seems to afford no evidence of a rapid or strongly pronounced climatic alteration, it becomes fairly probable that the more abrupt plant changes described in western Europe were induced chiefly by the sweeping orogenic effects of the Hercynian movement, rather than by a great climatic change of world-wide extent. This does not, however, preclude a moderate but far-reaching modification of climate, in which changes in the atmospheric composition may have played a subtle if not important part. It seems hardly possible that the tremendous amounts of carbon then being stored away in the coalfields as the result of plant extraction from the air could have failed to produce some effect on the atmospheric content of CO_2.

Though the Stephanian flora has less unity in its distribution than had the Westphalian, it is nevertheless remarkable for its geographical range. The flora reported by Zalessky[1] from the Yen-tai mines near Mukden in Manchuria embraces eight species, seven of which are found in western Europe, while six are present in the Appalachian trough. Or, looking southward, at Tete on the Zambesi in southern Africa, we find that all of eleven species reported by Zeiller are present in Europe and nine or ten, about 80 per cent., in America also. In harmony with these facts we find but slight traces of annual rings in the woods of the Stephanian, either in Europe or in America. This is the more noteworthy because the date of the Gondwana-land glaciation has been referred by various geologists to the Stephanian.

THE PERMIAN FLORAS

Floral characters.—The coming of the Permian is characterized not only by orogenic movements in the eastern hemisphere, but also by indications of increasing climatic differences. The first paleobotanical effect of these is the extinction of nearly all characteristic Carboniferous types, except in Pecopteris, Cordaites, and Neuropteris, the latter, however, disappearing nearly completely by the close of the Autunian or lower stage. They are replaced by varied forms of Callipteris, the lingulate Odontopteris and the ribbon-like Taeniopteris, together with expanding gymnospermous types, such as Walchia, Dicranophyllum, Doleropteris, Psygmophyllum, and Ginkgophyllum. Later, in the Saxonian, or Middle Permian, Voltzia, with the thick-leaved Equisetites, appears while more of the older types go out; and in the Thuringian, or Zechstein (Upper Permian) Rhipidopsis, Araucarites, Gomphostrobus, Voltzia, and Ullmannia, become the characteristic genera, while Pecopteris, dominant in the Stephanian, has nearly vanished. Though lacking the abundant Cycad and Cladophlebis-Asterocarpus elements, the Upper Permian is in many respects transitional to the older Mesozoic flora.

The Gangamopteris or lower Gondwana flora.—Meanwhile in the South a new flora, the Gangamopteris flora, or so-called Glossopteris flora, has arisen in the wake of retreating ice, though it is not really a glacial flora. It probably originated in a great region, the "Gondwana land" of Suess, from which the Stephanian flora had been more or less completely expelled by the rigorous climate, and to which it had not yet been able to return, presumably on account of either temperature or isolation.

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[1] *Verh. Russ. K. Min. Gesell.* (2), Vol. XLII (1905), p. 485.

The dominant characteristic types are Gangamopteris, Glossopteris, and its rhizome Vertebraria, Neuropteridium, Noeggerathiopsis, Phyllotheca, Schizoneura, Ottokaria, and Derbyopsis. The distribution and the relations of this flora to the Northern or Cosmopolitan flora have already been discussed in this journal.[1] The geographical extension of this flora in Paleozoic time, as also the distribution of the northern or cosmopolitan Permian flora, are shown on the Permian map, Fig. 2.

Distribution.—The uniformity of the Gangamopteris flora is so nearly complete as emphatically to indicate freedom of migration between all the areas in which it dominated; but whether Australia communicated with South Africa by way of India and Arabia, or by connection through an Antarctic land mass is a matter of opinion. The former is perhaps more probable. South America was almost certainly made accessible either to Africa or Australia by route over Antarctic land.

Gondwana climate.—The Gondwana climate following the glaciation was not too severe for the early return at distant points of a few of the presumably hardiest representatives of Psaronius, Sigillaria, Lepidophloios, and Lepidodendron, and at a higher stage, Voltzia Psygomophyllum, and Pterophyllum, both in Africa and South America. The early return of a climate not so widely different from that of the western Permian is further shown by the fact that though the early Gondwana woods found in beds more or less closely associated with the bowlder beds in Australia and South Africa show annual rings indicative of sharp seasonal changes, the woods from the higher portion of the series in South America show nearly continuous growth with but slight trace of seasonal differences.

Ability of types to mingle in later Permian and early Mesozoic environments.—This amelioration of temperature harmonizes, firstly,

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[1] *Jour. Geol.*, Vol. XV (1907), p. 615.

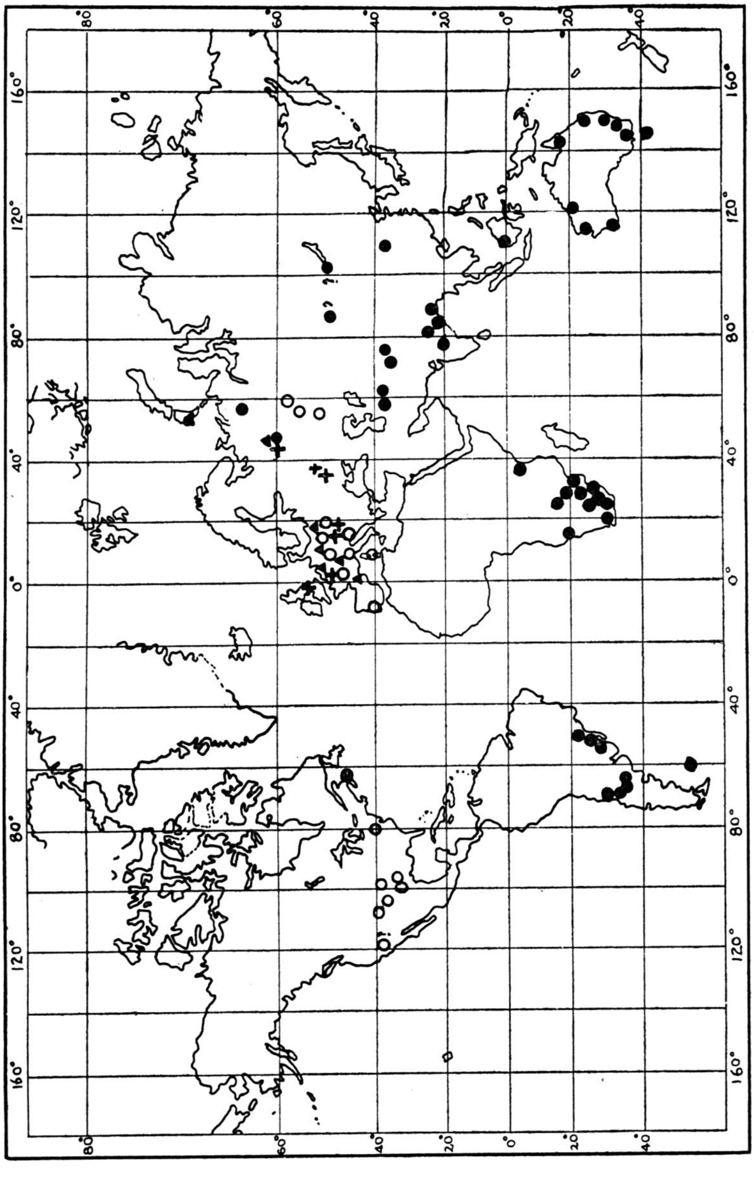

Fig. 2.—Regional distribution of Permian floras. White rings = Lower Permian; triangles = Middle Permian; crosses = Upper Permian; solid rings = Gondwana flora.

with the return of some of the northern types to portions of Gondwana land, and, secondly, with the fitness of some of the Gondwana types, especially Glossopteris, Phyllotheca, and Noeggerathiopsis, not only to join with Walchia and Callipteris in the Zechstein flora of northern Russia, but later to meet with Podozamites, Ctenophyllum, Cladophlebis, Clathropteris, and Dictyophyllum, under the mild climatic conditions of the early Mesozoic. Glossopteris, perhaps most adaptable of the older Gondwana types, was able to reach as far as the supposed Rhetic of Tonquin where it is last seen.

Glaciation.—It appears, therefore, that the interval, or better the *intervals*, of glaciation in Gondwana land were of relatively short duration as compared to all Permian time, though the thickness and distribution of the glacial deposits indicate a magnitude far exceeding that of Pleistocene glaciation. At the same time it seems improbable that refrigeration could have occurred in so many regions of the southern and eastern hemispheres, even approaching the equator, without some corresponding, though unequal, changes of world-wide extent. Concerning this very important point, the evidence is quite inconclusive and the opinions varied.

American Permian types derived from Europe.—If we compare the plants of eastern America with those of western Europe we find the greater changes in Europe where the extensive orogenic movements and attendant shifting of basins of deposition doubtless stimulated the evolution of the Permian flora. On the other hand, in the Appalachian trough, where environment was but little affected by orogeny, and where sedimentation was uninterrupted, there is only gradual change, many of the Stephanian types persisting far up in the Dunkard formation. The relatively few species characteristic of the European Permian which occur in the Dunkard, and which were not able to conquer the older flora under the conditions then existing, are clearly migrants from western Europe. It must be noted, though, that both West Virginia and Kansas exhibit new generic types, the products of local conditions, that have not been found outside of these regions. On the other hand, Walchia, which is present in Kansas and New Mexico has not yet been discovered in the Appalachian trough though it is present in the Nova Scotian basin, which seems to have been in closer touch with Europe at this time. The floral changes in the western American areas, which are more pronounced than in the Appalachian trough, may be due either to changed physical conditions consequent to nearer and greater orogenic movements, or possibly to position nearer to the region of Gondwana glaciation. In our trans-Mississippi region the contrast between the Permian and Stephanian floras does not seem so sharp as that between the Ural flora and those, for example, of the fresh-water basins of France or England.

Greater contrasts in eastern Europe.—In France and in the Appalachian trough the early Permian floras are to a large extent identical, thus indicating continued freedom of intercourse. Also the woods present obscure rings or none at all. But in Kansas and Texas annual rings while still but slight are increasing in distinctness though many of the associated plants have a European distribution.

The plant fragments from the Permian of Nova Zembla are quite too insufficient to support the hypothesis of a far-northern route of intercontinental migration, or even to show that the climate of western Europe extended so far north.

Ural Mountains on western edge of a great climatic zone.—Indeed, on the contrary, the great scarcity of true Neuropterid and Pecopterid elements, the great development of Psygmophyllum, and the remarkable phases of Callipteris observed even in the Artinsk of the Ural region indicate, in my judgment, either temporary isolation or an appreciable difference in climatic conditions. At the same time the somewhat unique forms of Odontopteris are not without representation both on the central plateau of France and in the Wichita of Texas. This testimony of migration is supported by the supposed land relations, which, if Lapparent is correct, should have been particularly favorable for such a migration during portions of Permian time.

Extension of Gondwana flora into northern Asia.—Eastward of the Ural Mountains the floras of the Altai and headwaters of the Yenesei and in northern Mongolia, though provisionally referred to the Permian on account of the presence of Rhipidopsis, mingled with other types, including some of Gondwana facies, are possibly wholly lacking in specific types characteristic of the Cosmopolitan Western Permian. Though the stage of these plant beds is not yet fixed on account of the strange character of the flora, I am inclined to regard the peculiar floral association as due to the extension of the early Gondwana climatic influence into north-central Asia and the subsequent isolation of the flora from western influences. This theory is supported by the presence of the older Gondwana flora in the coalfield of Shensi in China. On the other hand the floral differences between the Ural and eastern localities may be due to geographic position of the latter in the interior of the great Asiatic continent while the Ural flora which has more elements in common with the western world is located on the west coast of this continent.

The contrast is certainly not due to mere latitude, nor can it be credited wholly to aridity; for the eastern plants are associated in great series with coals in each region. A few stray wood fragments of uncertain location and age appear to offer slight evidence of seasonal changes, but the criteria deserve careful re-examination both as to this point and as to the geological horizon of the material described.

It would be most interesting to know to what extent the plant life of Permian time on the west coast of North America was influenced by the Gondwana glacial climate and as to how far it was allied to the older Gondwana floras.

The sharp contrast between the Chinese Gondwana plants and the floras of the very latest Stephanian in the same region involves a pronounced break either in climate or in time in that quarter of the globe. Probably both are concerned. The most satisfactory illumination of the stratigraphical and paleontological history of this period will probably be found in China or southern Siberia.

"PERMO-CARBONIFEROUS CLIMATES"

Climate of the Carboniferous.—The climate of the Pennsylvanian ("Upper Carboniferous") as viewed in perspective was mild and relatively humid, and, above all, equable over the greater part of the earth. It was moderate in temperature, not tropical, possibly not even subtropical, but, during the Westphalian at least, always and everywhere equable. It was truly temperate. The criteria which may be interpreted in support of this generally accepted proposition include:

1. The tremendous size and great height of the types, and their rank foliar development, indicating favorable conditions of environment and vigorous nutrition.

2. The succulent nature of many of the forms, the large size of the vessels and cells and the relatively great proportion of soft tissue, all indicating rapidity of growth in a moist, mild climate.

3. Spongy leaves suggestive of a moist atmosphere, and abundant and large intercellular spaces, as in the Lycopods, pointing to rapid moisture loss; also water pores for disposal of excess of moisture.

4. Stomata placed in grooves, as in the Lycopods, as if to prevent obstruction by falling rain.

5. Absence of annual rings in the woods; hence absence of marked seasonal changes.

6. The analogies of the present day show that aërial roots, so prominent in many of the Carboniferous types are characteristic of moist and tropical climates; that the nutrition—i. e., the decom position of CO_2—is most rapid and the consequent growth also greatest and most rapid where the light is not too strong; that the ferns and Lycopods, so abundant in the Paleozoic, usually avoid bright glare. The same types are able to withstand larger amounts of CO_2 with benefit to themselves.

7. The nearest living relatives of the Paleozoic vascular Cryptogams reach their greatest size in humid and mild or warm climates. The successors of the marratiaceous, and gymnospermous types are now mostly confined to tropical or subtropical regions. The cycadalean stock, now characteristic of the same zones, was actually present in the upper coal-measures.

8. The formation of great amounts of coal indicates a rank growth, but in a temperature not so warm as to promote decay beyond the limit of rainfall protection.

9. Living nearest representatives of Paleozoic fishes now inhabit the estuaries of warm countries; while the nearest relatives of the Carboniferous insects are now found in mild and moist habitats.

10. The most forcible argument, after all, for an equable and uniform climate lies in the extraordinary geographical distribution of the floras in relative unity over the face of the earth. Humidity must naturally have attended such equability, extending, without

distinct terrestrial climatic zones, possibly completely into the polar regions.

Some of the criteria above mentioned are susceptible of different interpretations; but taken collectively they appear to admit of but one conclusion. Whether or not we admit that climatic changes may be caused by reasonable or practicable changes in the amount of carbonic-acid gas in the air it is certain that in geological times the vegetation of the earth must have been more or less influenced by the constitution of the atmosphere from which the plant derives so important a part of its real food.

Gradual loss of uniformity of climate, with brief glacial interruption in Permian.—As has already been indicated the Westphalian probably witnessed the greatest extension of uniformity and equability of climate over the earth. In the Stephanian the flora is hardly so homogeneous, though the world-climate appears still to have been so equable as to allow free migration of the larger part of the flora from a moderate latitude on one side of the equator to the opposite without encountering seriously obstructive seasonal changes. In the Permian the regional distinctions between the floras are much clearer; and presently climatic zones, and consequently botanical provinces, are recognized. Yet, about the North Atlantic the climate of the Lower Permian was still relatively uniform so that moderately free migration of the floras without the development, so far as we know, of pronounced annual rings, took place in the Autunian of France, the Permian of Prince Edward Island, the Dunkard of southwestern Pennsylvania, the Chase of Kansas, and the Wichita of Texas.

Red beds and climate.—It will be remembered that the period now considered is characterized in western Europe, England, Eastern Canada, the Appalachian trough, and the Western Interior basin, by the deposition of red beds which in some areas carry deposits of gypsum, etc., and which are generally regarded as laid down under an arid climate. Viewing the matter from the paleobotanical standpoint, we may ask whether equability and uniformity of climate, such as is shown by the fossil floras, is compatible with aridity in latitudes so high as northern England and the Gulf of St. Lawrence. If all the regions of Permian red-bed deposition were arid it would seem that humidity could not have been essential to equability of climate.

Coal-formation in Permian.—The lower Permian of Germany, France, Russia, and Pennsylvania, is commercially coal-bearing, while the Permian red beds of Kansas and Texas carry thin coals. Professor C. A. Davis informs me that in the United States today the formation of peat, the first stage of coal, is practically confined to the zone having twenty inches, or more, of rainfall.

Flora in red beds not perceptibly different from that in other sediments.—The plants in the Monongahela and Conemaugh do not seem to differ in kind whether the series are gray and limestone-bearing in Pennsylvania, or red and nearly devoid of limestones seventy-five miles to the south in West Virginia; except that although sometimes fairly abundant, they are very difficult to find in the red shales because the carbon of the plants is almost or entirely gone, as the result of destructive decomposition, only impressions of the leaves being left. Is it not possible that, in some instances, the causes of red-bed deposition lie to a large extent in relatively slow subsidence of the basin, and in differential warping to permit exposure, with some redeposition and dehydration? It is probable that there was aridity in certain regions and during certain intervals of the Permian; but there was evidently enough moisture to produce most extensive glaciation, and, later, to promote the formation of coals over broad areas in the great fresh-water Gondwana series laid down on the continents of South America, Africa, and Asia. The beds with the Gangamopteris flora are in most regions coal-bearing, usually commercially.

Date of glacial episode.—If one looks for climatic fissures, or dislocations into which to fit the relatively brief episode of Gondwana glaciation it is difficult either in western Europe, or in America, to find an opening between the base of the Westphalian and the top of the Lower Permian in which it may be fixed. It is true that, in most sections, we have intervals in which no plants are found; and, further, the lesson of Pleistocene deposition shows what sweeping climatic changes may occur and recur within a relatively insignificant thickness of strata. Yet, while the gap is often large enough in stratigraphical view, the plant-sequence so tightly closes it as to preclude a possible very distant exile of the flora for a time. We may therefore conclude that the glacial episodes probably occurred at the time of one of the orogenic movements; and, if so, preferably at one marked by the most striking floral changes, since the effects of so important a climatic event must have been widespread.

If, therefore, the glacial interruption did not occur at the close of the Mississippian, as Bodenbender seems to see it, we may, I think, continue provisionally to regard it as occurring at the close of the Stephanian, or possibly (as would better suit many of the facts) as late as the middle Permian. The totally unaffected aspect of the topmost Stephanian flora near Mukden in Manchuria and in Italy, as well as of the somewhat earlier Stephanian flora in South Africa, would, if evidence of other kinds to the contrary were absent, tend somewhat strongly to prejudice in favor of the later date. The moderate temperature of the fairly equable "Permo-Carboniferous" climate in general may explain why the shock of the climatic episode was not more severely and for a longer time felt by the cosmopolitan Permian flora of western Europe and America.